

Nestling diet and feeding rates of Rhinoceros Auklets in Alaska

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1. Abstract

Food brought to nestling Rhinoceros Auklets (*Cerorhinca monocerata*) was sampled by applying tape or cloth muzzles to the chicks and collecting the uningested food from the burrow daily. Limited data were also gathered for Tufted and Horned puffins (*Fratercula cirrhata* and *F. corniculata*). Auklet chicks received an average of 34.1 g of food per night at Middleton Island in 1978, and 32.8 g per night at the Semidi Islands in 1979. Pacific sandlance (*Ammodytes hexapterus*) made up the bulk of the diet at both locations, and large, second-year or older fish predominated in the samples. In contrast, Horned and Tufted puffins took mostly small, first-year fish during the same seasons. The quantity of food delivered per night to Rhinoceros Auklets increased with the age of the chick, and wind speed may have been an important environmental factor affecting feeding rates. Proportions of first-year and older sandlance in the diet varied within and between sampling bouts, indicating spatial and temporal changes in prey availability. Parallel changes in feeding rates were also observed. The primary use of different age groups of sandlance by the three puffin species suggests the age structure of the prey population may differentially affect breeding success.

2. Résumé

Nous avons échantillonné la nourriture apportée à de jeunes Alques à bec cornu (*Cerorhinca monocerata*) par l'application de muselières faites de ruban adhésif ou de tissu aux oisillons et par la collecte quotidienne des aliments non ingérés se trouvant dans le terrier. Nous avons également réuni un certain nombre de données pour les Macareux huppés et les Macareux cornus (*Fratercula cirrhata* et *F. corniculata*). Les jeunes alques ont reçu en moyenne 34,1 g de nourriture par nuit à l'île Middleton en 1978, et 32,8 g par nuit aux îles Semidi en 1979. Le lançon du Pacifique (*Ammodytes hexapterus*) compose le gros du régime alimentaire aux deux endroits et les gros poissons âgés de deux ans ou plus dominant dans les échantillons. En revanche, les Macareux huppés et les Macareux cornus ont généralement capturé de petits poissons d'un an au cours des mêmes années. La quantité de nourriture livrée chaque nuit aux jeunes alques augmente en fonction de l'âge du juvénile. La vélocité du vent peut avoir été un facteur environnemental important influant sur les taux d'alimentation. Les proportions de lançons âgés d'un an et plus dans le régime varient d'une période d'échantillonnage à l'autre et dans une même période, ce qui témoigne des variations

spatio-temporelles de la disponibilité des proies. Nous observons également une évolution parallèle des taux d'alimentation. Les principales utilisations des divers groupes d'âge de lançon par les trois espèces de macareux donnent à penser que la structure d'âge des proies peut différemment influencer sur la réussite de la reproduction.

3. Introduction

Recent studies on the breeding biology of puffins have generated considerable information on foods and feeding ecology during the chick period. The Atlantic Puffin (*Fratercula arctica*) is especially well known in this respect (Pearson 1968, Nettleship 1972, Corkhill 1973, Harris 1978, Hudson 1979, Ashcroft 1979), whereas three North Pacific species, including the Rhinoceros Auklet (*Cerorhinca monocerata*) (Storer 1945), have received comparatively little attention. Information is available for Rhinoceros Auklets and Tufted Puffins (*Fratercula cirrhata*) at colonies in Washington (Cody 1973, Leschner 1976, Wilson 1977) and British Columbia (Vermeer 1979; Vermeer *et al.* 1979; Vermeer and Westheim, this volume; Summers and Drent 1979). Information for Alaska, where large numbers of all three species breed, has only recently become available (Amaral 1977, Wehle 1980).

Results of investigations on puffins support three general conclusions: (1) the food delivered to chicks usually includes very few species of prey at any one place and time; (2) nestling diets commonly exhibit annual, geographic, and seasonal variation, which presumably reflects changes in the availability of potential prey; (3) such variation affects chick growth and survival, and therefore reproductive success.

This paper is based on food samples collected in 1978 and 1979 at two colonies of the Rhinoceros Auklet in Alaska. The main objectives are (1) to examine variation in the nestling diet of this species, along with supplemental information for the Tufted Puffin and Horned Puffin (*Fratercula corniculata*); (2) to identify factors that affect feeding rates in the Rhinoceros Auklet; and (3) to suggest some possible effects of prey population structure on the breeding ecology of puffins.

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4. Study areas

The two study sites are about 700 km apart in the central and western Gulf of Alaska. Middleton Island lies in the path of the Alaska Current (Favorite *et al.* 1976), 90 km from the Alaska mainland and 20 km from the edge of the continental shelf (Fig. 1). The island measures about 1.5 by 8 km and is used by seven species of breeding seabirds totalling around 175 000 individuals. In 1978, Rhinoceros Auklets occurred in four well isolated subcolonies totalling some 1800 birds. An estimated 3000–5000 Tufted Puffins nested at low density around much of the perimeter of the island. Food samples of both species were collected at several points around the island. No Horned Puffins breed on Middleton Island.

The Semidi Islands include nine islands and numerous smaller islets and rocks 80 km south of the Alaska Peninsula near longitude 156° W. The edge of the continental shelf lies some 80 km to the south. Collectively, these islands support the largest breeding aggregation of marine birds in the Gulf of Alaska (2.4 million birds of 20 species), although Rhinoceros Auklets are relatively uncommon (Sowls *et al.* 1978). They are known to breed only on Chowiet Island where they number about 800 birds. Tufted Puffins (100 000) and Horned Puffins (375 000) nest on all islands in the group. Food samples of these species were collected primarily at Kateekuk Island, 2 km to the northwest of Chowiet, and at Suklik Island, 3 km to the east.

5. Methods

5.1. Field technique

Food samples were obtained primarily by applying a muzzle to the chick to prevent it from swallowing any of the food delivered by its parents, and collecting the accumulated food from the floor of the nest chamber daily. At Middleton Island, fibre-reinforced packaging tape was folded and tied in a harness around the bill and back of the head (Baird and Moe 1978). Boot-shaped cloth hoods were used to cover the entire head at the Semidi Islands. Three sizes were sewn to fit chicks of various ages. A draw string of yarn around the lower margin, tied at the nape, prevented the hood from slipping off. Hoods were preferable to tape because they caused less stress and, unlike tape, were never removed by the chicks. The procedure was also more efficient because hoods were reusable and simpler to apply. I refer to food samples collected by this method as "burrow-loads"; samples collected directly from adults (e.g. Nettle-ship 1972, Corkhill 1973) I call "bill-loads."

Collections were made in four sampling periods 6–7 days apart at Middleton Island (18 July – 16 August 1978), and in three sampling periods 10–13 days apart at the Semidi Islands (18 July – 11 August 1979). A sampling period comprised two successive nights, i.e. each chick wore a muzzle for 36–48 h, but samples were collected each morning. Because Rhinoceros Auklets visited their nests only at night, each sample represents the quantity of food delivered to a chick in a 24-h period. Chicks were weighed at the outset of each sampling period and after each interval of fasting. Their ages were estimated from wing measurements on the first visit with reference to data for known-age chicks (Leschner 1976).

The method I have described had only limited success with Tufted and Horned puffins. Samples obtained

from these species were supplemented with bill-loads or specimens of prey found on the ground near burrow entrances, but the total of material available for comparison with the auklets is minimal.

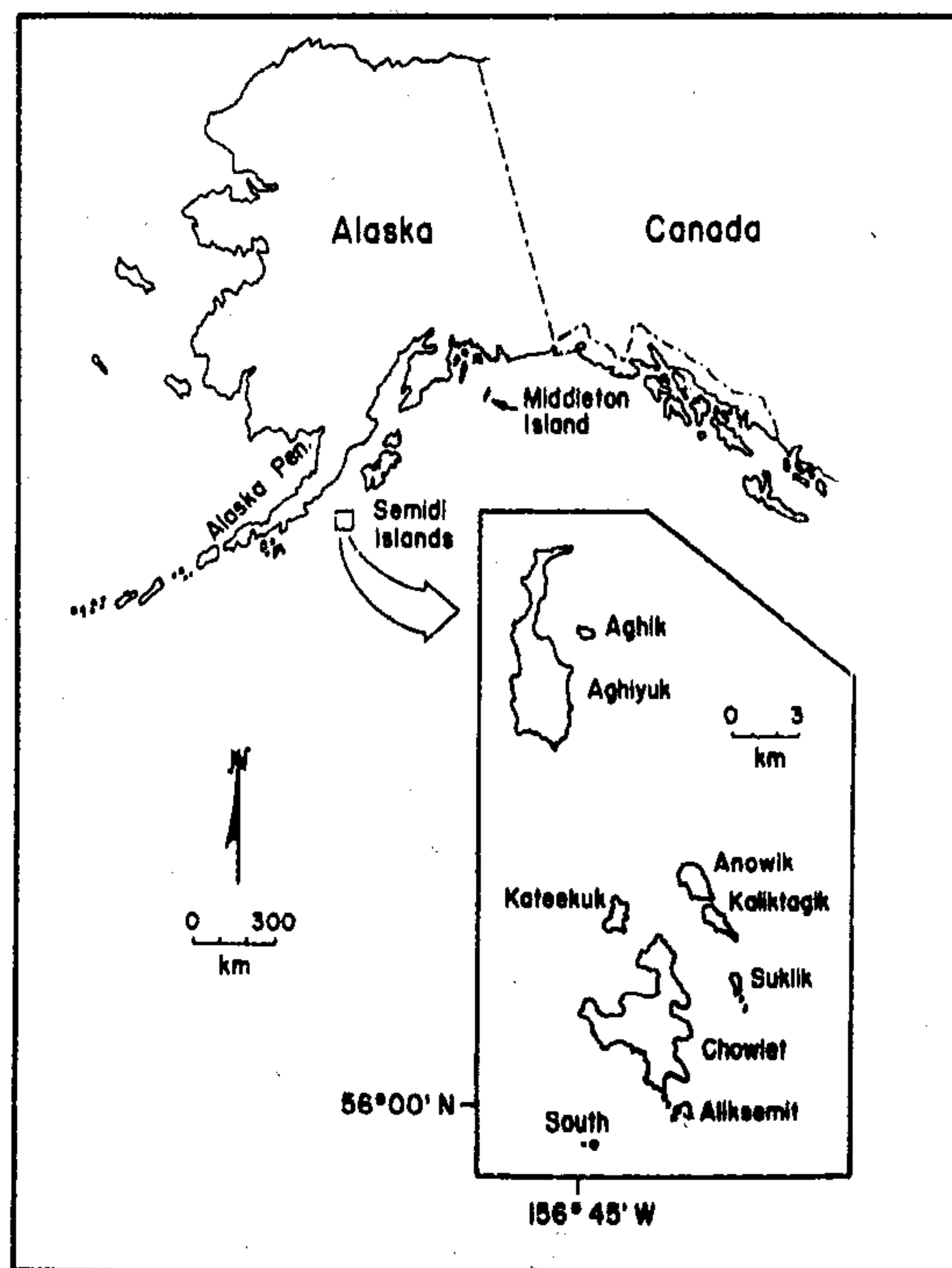
5.2. Laboratory technique

Food samples were preserved in 10% Formalin for later sorting and identification of species in the laboratory. Except as noted below, identifications were made by the author. Fish lengths were measured to the nearest millimetre from the snout to the tip of the tail. Age-classes of sand lance (*Ammodytes hexapterus*) were assigned by inspection of the distribution of lengths in my sample and distributions for known-age fish (Blackburn 1979; Dick and Warner, in press). Preserved burrow-loads were air dried for 2–3 min and weighed with a triple beam balance accurate to 0.1 g.

5.3. Statistical analysis

Most of the statistical analysis was accomplished using the SPSS package of computer programs (Nie *et al.* 1975). I used the arcsine transformation on percentages and an additional transformation ($Y \rightarrow Y^2$) on two variables (proportion of sand lance per burrow-load and relative proportion of second-year or older sand lance) to yield distributions with nonsignificant skewness and kurtosis.

Figure 1
Location of study sites in the Gulf of Alaska



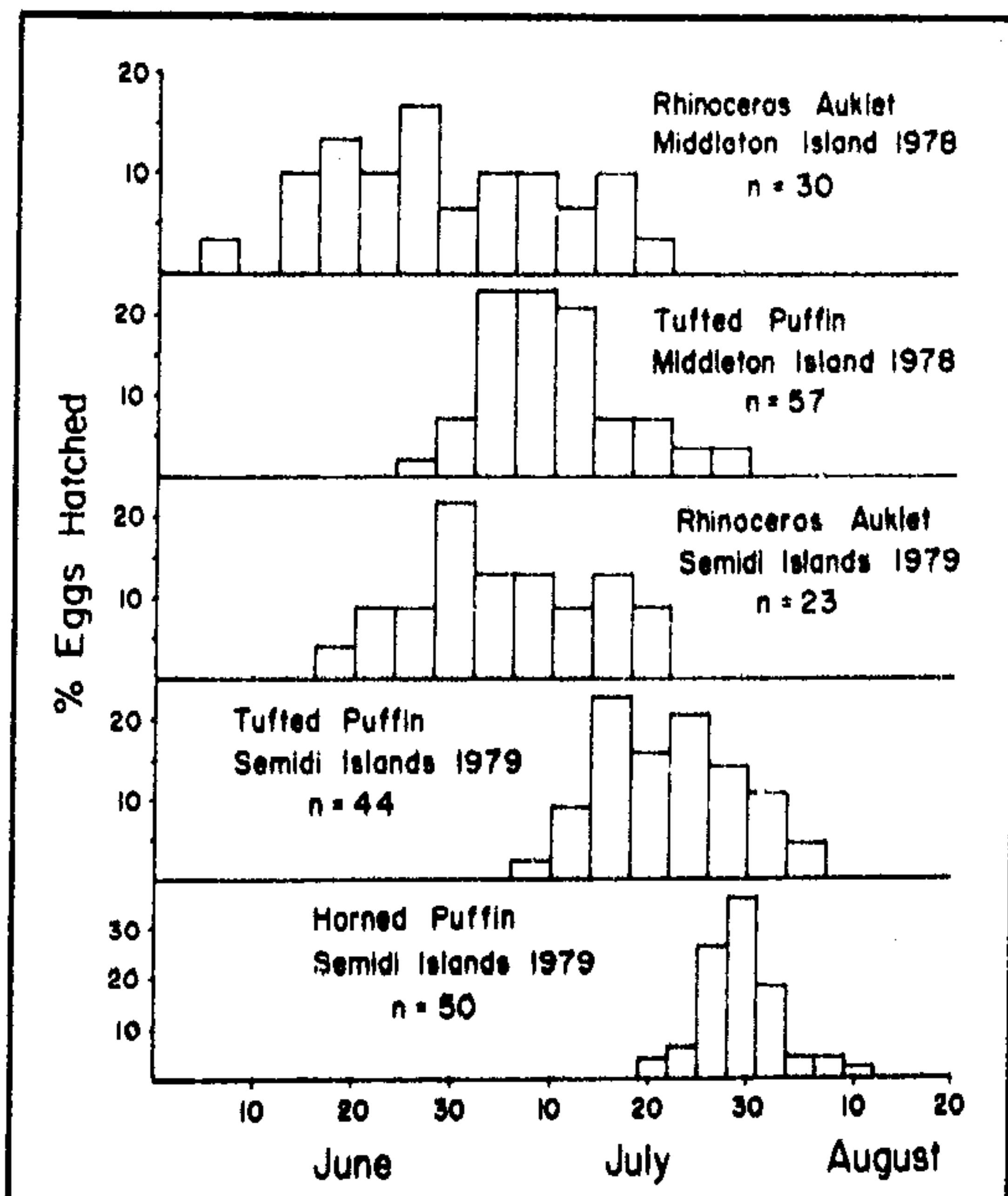
6. Results

6.1. Breeding phenology

Since the food available to seabirds varies seasonally and annually, it is useful to note differences in the timing of breeding among the three puffins. Rhinoceros Auklets probably breed earliest wherever these species occur together (Fig. 2; see also Vermeer *et al.* 1979). At Middleton Island their eggs hatched about 2 weeks earlier than those of Tufted Puffins, and at the Semidi Islands, about 3 weeks earlier. Horned Puffins, in turn, hatched 1 week later than Tufted Puffins at the Semidis. Breeding schedules were earlier at Middleton Island in 1978 than at the Semidis in 1979, about 1 week for Rhinoceros Auklets and 2 weeks for Tufted Puffins.

The fledging periods of Rhinoceros Auklets, Tufted Puffins, and Horned Puffins average 51, 47, and 40 days, respectively (Vermeer and Cullen 1979, Wehle 1980). The mean age of Rhinoceros Auklet nestlings from which food samples were collected was 33.1 days at Middleton Island ($n = 68$, $sd = 11.0$, range 3–54 days) and 28.1 days at the Semidis ($n = 82$, $sd = 10.7$, range 13–52 days). Tufted Puffins averaged 24.4 days old in the sample on Middleton Island ($n = 16$, $sd = 8.1$, range 10–33 days). Since only bill-loads were obtained from Tufted and Horned puffins at the Semidis, the ages of chicks in the sample can only be approximated from sampling dates and the distribution of hatching (Fig. 2). The mean age of Tufted Puffins would have been in the range 30–35 days; the mean for Horned Puffins was probably 20–25 days.

Figure 2
Hatching dates of puffins at Middleton Island in 1978 and the Semidi Islands in 1979



6.2. Feeding rates

The distribution of burrow-load-size for Rhinoceros Auklets did not differ significantly from the normal distribution at either study area (Kolmogorov-Smirnov test for goodness-of-fit, $P > 0.05$). Means and ranges of load-sizes were similar at the two sites (Table 1). Body weight, averaged over all sampling periods, was 270 g per chick at Middleton Island and 225 g per chick at the Semidi Islands. Thus, the rates of food intake can be expressed as 12.6% and 14.6% of body weight per day at the two sites, respectively. Muzzled chicks lost weight at an average rate of 8.6% of body weight per day.

The feeding of Tufted Puffins was severely disrupted by the same collecting technique that appeared to work well with Rhinoceros Auklets (Table 1, Appendix). No food was delivered to Tufted Puffins on over two-thirds of days compared with 16% and 11% of days, respectively, for Rhinoceros Auklets at Middleton Island and the Semidis.

6.3. Nestling diets

Rhinoceros Auklet nestlings at Middleton Island were fed almost entirely Pacific sandlance, plus small quantities of four other species of fish as well as squid and octopus (Fig. 3, Table 2). Sandlance also made up the bulk of the diet at the Semidi Islands (Fig. 4), but capelin (*Mallotus villosus*) made up 29% by weight in mid July, declining thereafter (Fig. 5). Capelin were lacking at Middleton Island, and there were no notable changes in the composition of the diet during the season. Although data for Tufted and Horned puffins are limited, they suggest marked differences between the diets of these species and that of Rhinoceros Auklets (Figs. 3 and 4). Tufted Puffins, in particular, had important prey other than sandlance, including cephalopods at Middleton Island and walleye pollock (*Theragra chalcogramma*) at the Semidis. Larval flatfish (mean length 35 mm) and a euphausiid, *Thysanoessa spinifera* (mean length 30 mm), occurred in several samples at the Semidis. Although these items were not quantitatively important, it is notable that such tiny prey were brought to

Table 1
Performance of the food sampling scheme at Middleton Island in 1978 and the Semidi Islands in 1979

Variable	Middleton Island		Semidi Islands
	Rhinoceros Auklet	Tufted Puffin	Rhinoceros Auklet
Effort, chick-days	101	68	95
No. days chick died or disappeared	11 (10.9%)	8 (11.8%)	0
No. days chick removed muzzle	9 (8.9%)	11 (16.2%)	3 (3.2%)
No. days no food delivered*	13 (16.0%)	33 (67.3%)	10 (10.5%)
No. loads collected	68	16	82
Weight per load, g			
mean†	30.6	13.1	36.4
sd	16.5	15.2	17.8
range	9.9–81.3	3.7–57.8	6.5–80.5
Overall feeding rate, g day ^{−1}	34.1		32.8

*Percentages calculated after excluding instances in which the technique failed because the chick was lost or removed its muzzle

†Mean for all sampling periods combined

‡Rates include nights on which no food was delivered

chicks. Similarly, one bill-load of a Horned Puffin consisted of 50 larval Osmerids, probably capelin, weighing less than 4 g in all.

Figure 3
Nesting diets of Rhinoceros Auklets and Tufted Puffins at Middleton Island, 26 July – 16 August 1978. Sample sizes are the number of burrow-loads

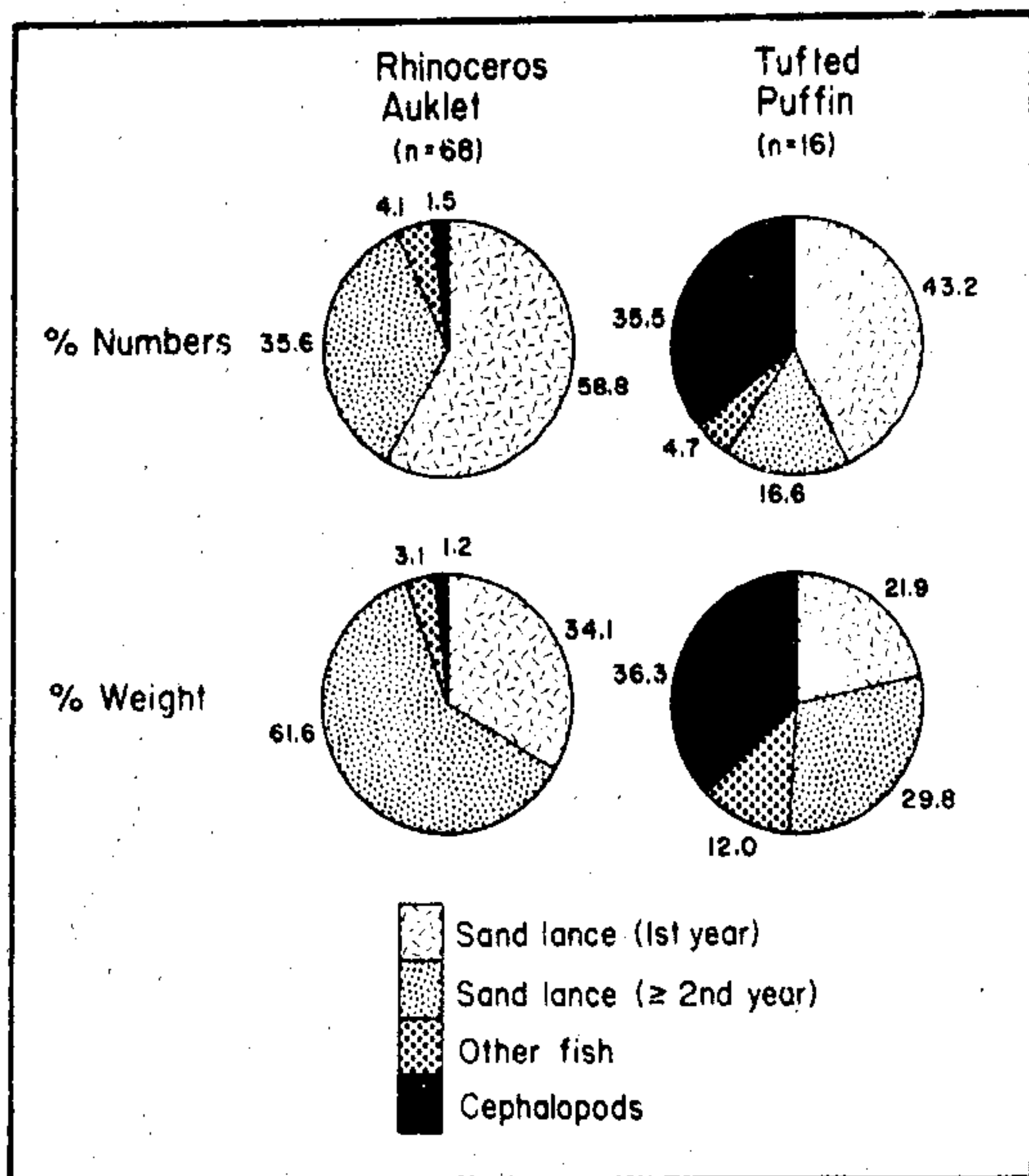


Figure 5
Temporal changes in the diet of Rhinoceros Auklets at the Semidi Islands in 1979. Samples are the number of burrow-loads

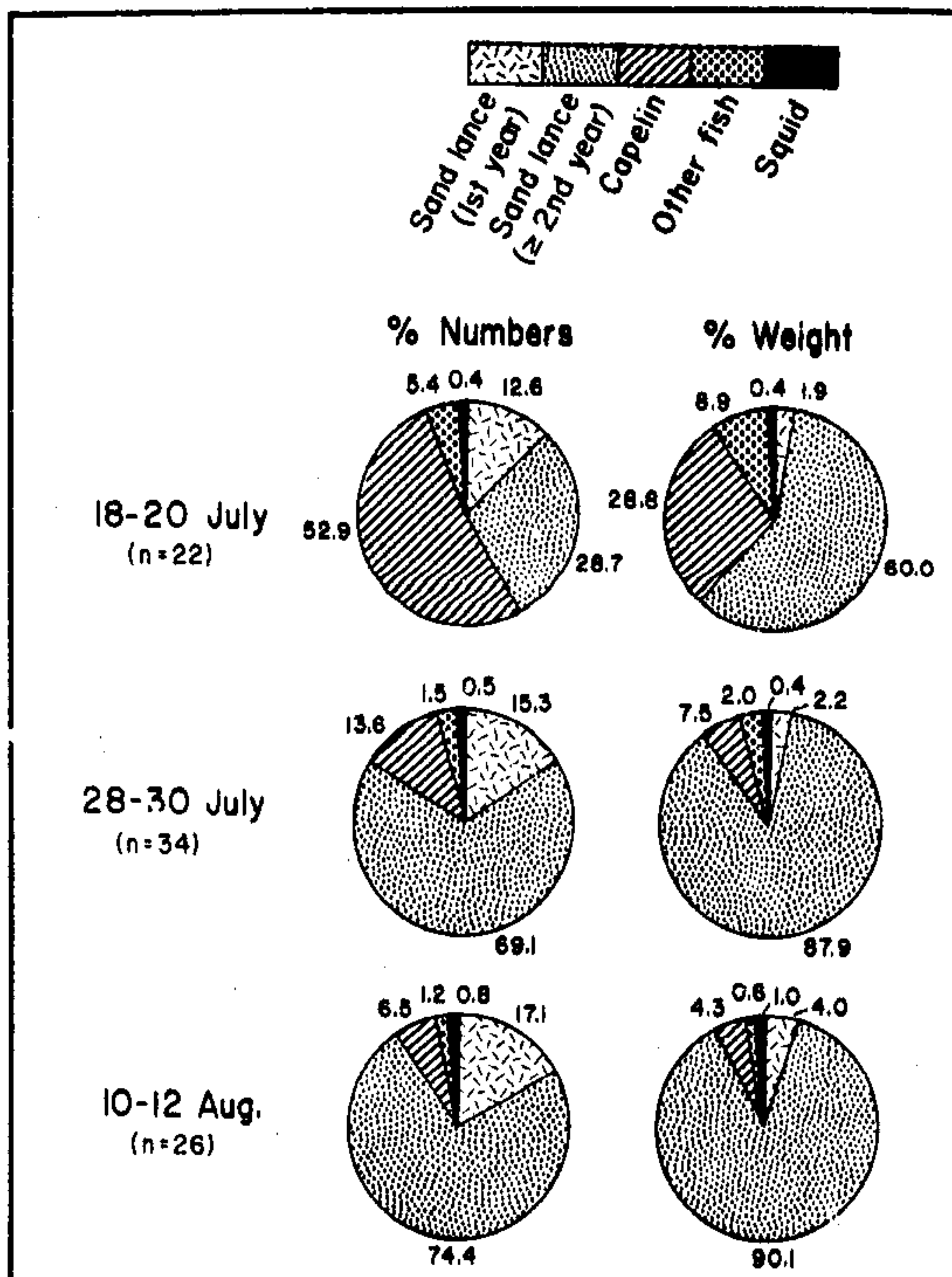
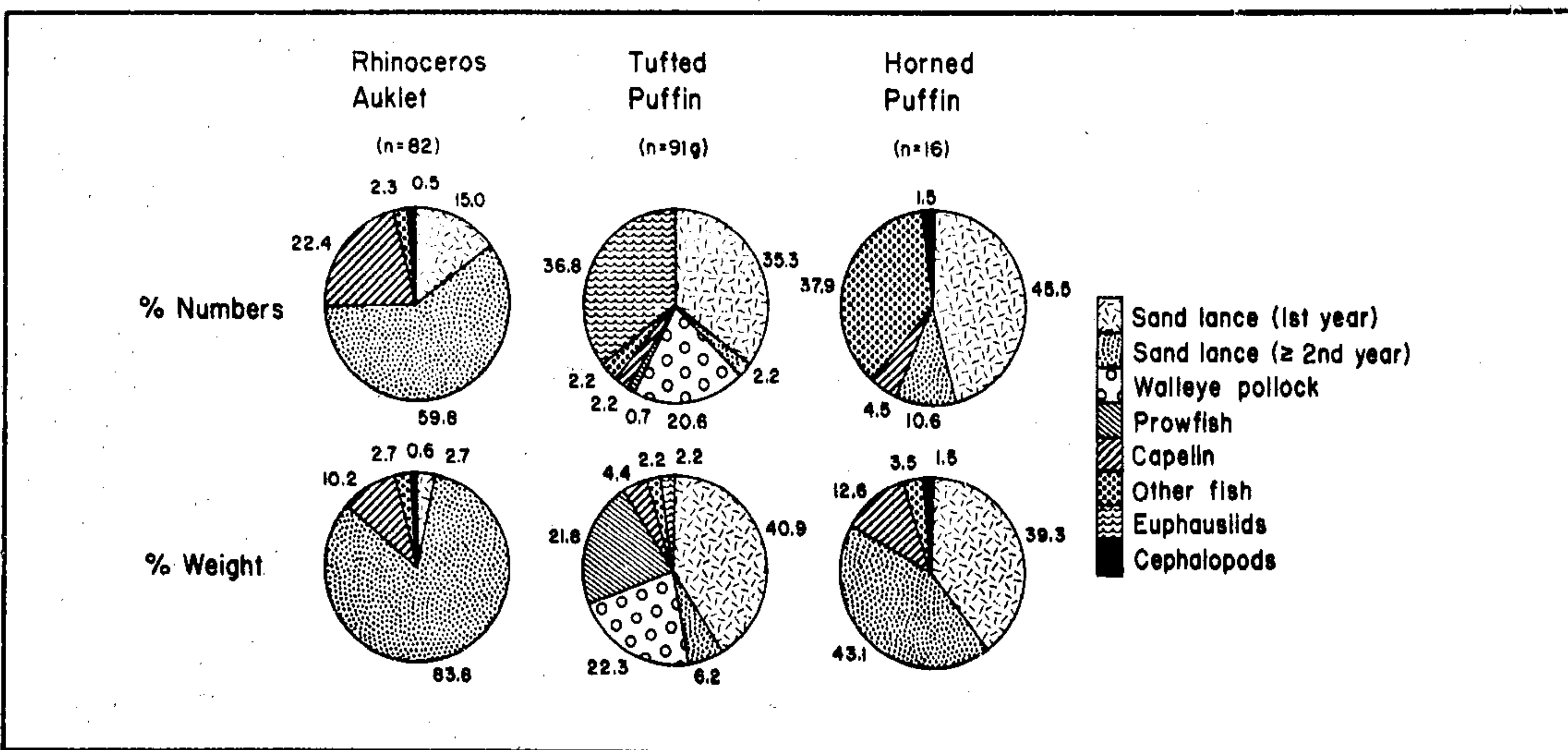


Figure 4
Nesting diets of Rhinoceros Auklets, Tufted Puffins, and Horned Puffins at the Semidi Islands 18 July – 11 August 1979. Samples are burrow-loads for Rhinoceros Auklets, bill-loads for Horned Puffins, and pooled material from various sources for Tufted Puffins



Two distinct size-classes of sandlance were present in the food samples (Figs. 6 and 7), and their relative importance differed markedly between species and between study areas (Figs. 3 and 4). According to Blackburn (1979), the smaller fish (first-year) would have hatched within the current year, probably in January or February, whereas most of the larger fish (second-year) were hatched a year earlier. The two largest fish (150–170 mm) collected at Middleton Island were probably 3–5 years old, and this group seemed well represented at the Semidis.

Measurable growth occurred in the youngest sandlance during the sampling period at each site (Figs. 6 and 7). The rate of increase in mean body length was estimated by linear regression to be 18.7 mm per month at Middleton Island and 21.0 mm per month at the Semidis ($P < 0.001$ for both regressions, $r = 0.554$ and 0.768 , respectively). These rates did not differ significantly, as shown by an analysis of covariance ($P = 0.225$). When age-classes are compared between the two sites, however, differences in overall mean length are evident in first-year and older fish alike (Fig. 8).

6.4. Analysis of variation in feeding rates

6.4.1. *Heterogeneity of load-sizes* — There was much variation in the weight of burrow-loads collected on a given night and in mean load weights on different nights (Fig. 9). A nested analysis of variance, with corrections for unequal sample sizes on different nights (Sokal and Rohlf 1981: 293), indicated that 60–80% of the variation in load-sizes occurred within nights, but about 20% occurred between nights (Table 3). No additional component of variance between sampling periods was found to account for variation between nights. However, because a seasonal increase in feeding rates occurred (see below), significant variation between periods would be evident had more sampling periods been included.

6.4.2. *Factors affecting feeding rates* — A number of factors might contribute to variation in feeding rates, including: (1) the age of the chick; (2) annual and seasonal changes in food availability; and (3) environmental variables such as wind or tides. The prevalence of sandlance in the diet of

Rhinoceros Auklets suggests the composition of samples is usefully characterized by the proportion of sandlance per load and the relative proportions of the two size-classes. Since prey other than sandlance were scarce at both study areas, and many loads at the Semidis contained only second-year or older fish, skewness in the distributions of these variables was not eliminated by transformation. I excluded, therefore, samples consisting entirely of sandlance or entirely of second-year fish from the following correlation analysis.

Simple correlation coefficients between burrow-load-size and several of the above variables indicate that none of the relationships is particularly strong (Table 4). Most are statistically significant, however, and I would expect factors causing feeding rates to vary by 5–10% to have biological significance as well. Table 4 also reveals significant correlations among independent variables which could lead to spurious conclusions about their individual effects on load-size. At the Semidi Islands, for example, sampling date was strongly correlated with the ages of chicks in the sample. When the apparent effect of sampling date on load-size is removed by partial correlation, there still is a significant positive relationship with the age of the chick, but the reverse is not true (Table 5). Thus, the size of burrow-loads increased with the age of the chick, but no seasonal trend in food availability can be inferred.

The proportion of sandlance per load and the relative amounts of the two size-classes were correlated with sampling date and the age of the chick (Table 4). Here again, partial correlations, in which the effects of sampling date and chick-age were controlled, revealed these relationships to be real (Table 5). This conclusion is strengthened by a comparison of means between samples consisting entirely of sandlance and those containing other prey. Pure loads of sandlance averaged 11.8 g at Middleton and 10.8 g at the Semidis, compared with 35.6 g and 33.3 g, respectively, for loads of mixed species composition ($P < 0.10$ in each case, t -tests). Similarly, loads containing only large sandlance averaged 7.7 g heavier than loads containing both age-classes at the Semidis (11.1 vs 33.4 g, $P < 0.15$).

The relation observed at Middleton Island between chick-age and the relative proportions of large and small sandlance was highly significant ($P < 0.01$), even when all

Table 2
Prey species and their percent frequency of occurrence in food samples

Species	Middleton Island		Semidi Islands		
	Rhinoceros Auklet ($n = 68$)	Tufted Puffin ($n = 16$)	Rhinoceros Auklet ($n = 82$)	Horned Puffin ($n = 10$)	Tufted Puffin ($n = 91$)
Pacific sandlance					
First-year	92.6	75.0	20.3	63.6	present
Second-year	92.6	37.5	89.0	36.4	present
All ages	92.6	81.3	92.7	81.8	present
Capelin			47.6	18.2	present
Larval Osmeridae				9.1	
Pacific sandfish (<i>Trichodon trichodon</i>)	11.8	6.3			
Kelp greenling (<i>Hexagrammos decagrammus</i>)	10.3				
Unid. Hexagrammidae			12.2		
Prowfish (<i>Zaprora silenus</i>)		12.5			present
Sablefish (<i>Anoplopoma fimbria</i>)	4.4				present
Walleye pollock					present
Rockfish (<i>Sebastes</i> sp.)	7.4		3.7		present
Larval Pleuronectidae					
Squid (<i>Gonatus middendorfi</i>)	7.4	43.8	4.9		
Octopus (<i>Octopus</i> sp.)	7.4	43.8		9.1	
Euphausiidae					present

Figure 6
Length frequency distributions of Pacific sandlance in the diet of Rhinoceros Auklet nestlings, Middleton Island, 1978. Fish in the stippled area were assigned to the first-year age-class; fish in the unshaded area were considered second-year or older

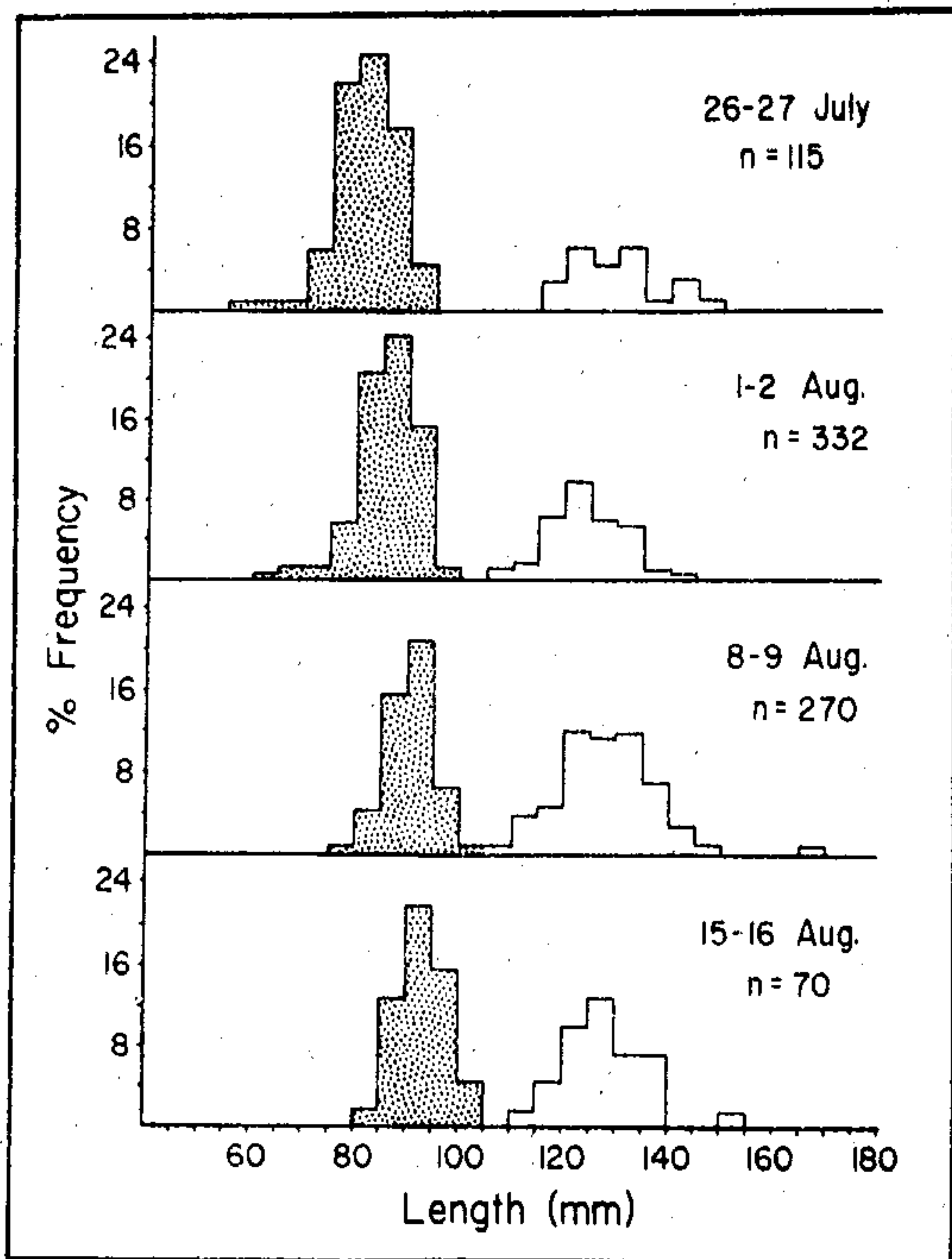
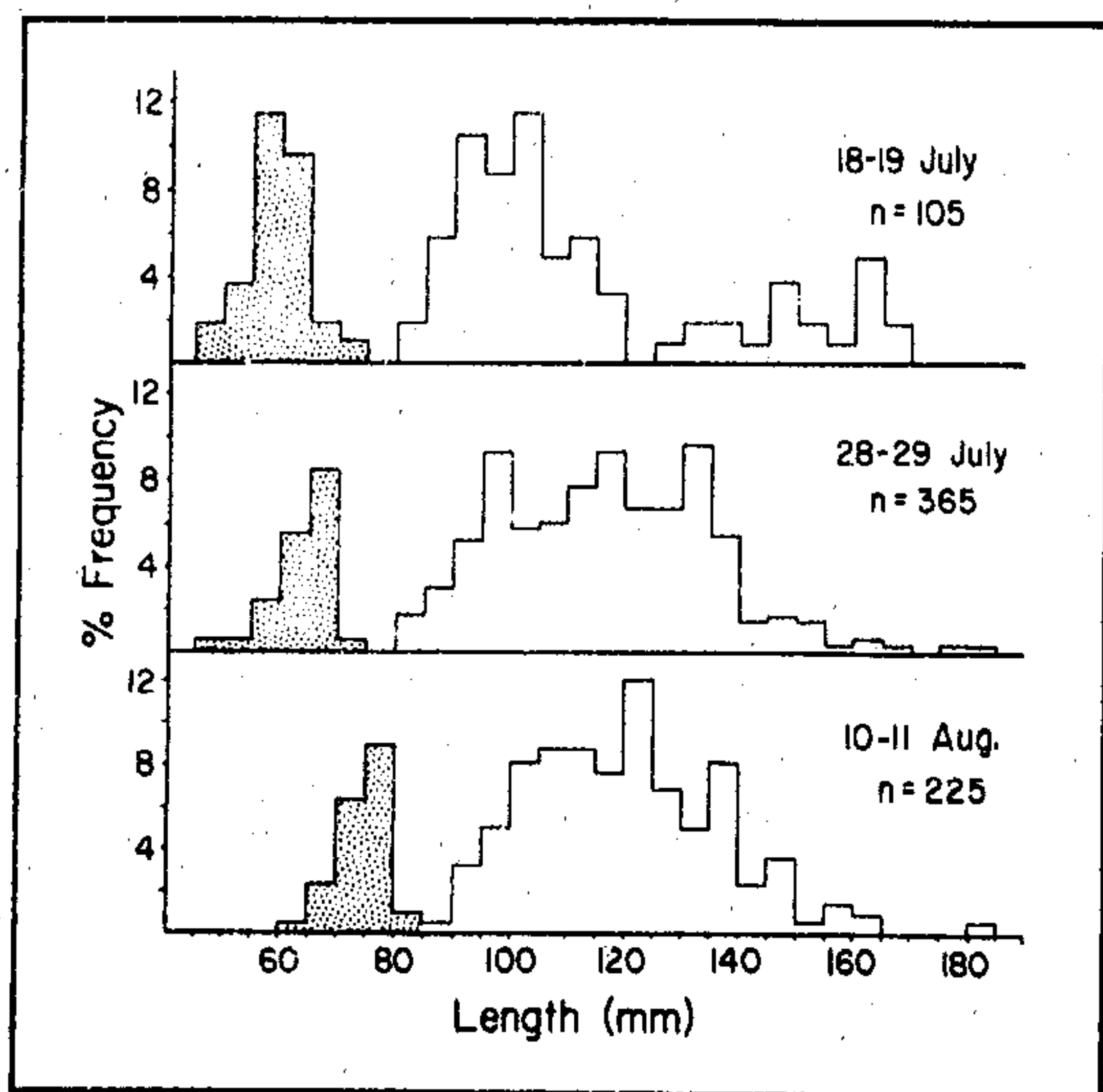


Figure 7
Length frequency distributions of Pacific sandlance in the diet of Rhinoceros Auklet nestlings, Semidi Islands, 1979. Fish in the stippled area were assigned to the first-year age-class; fish in the unshaded area were considered second-year or older

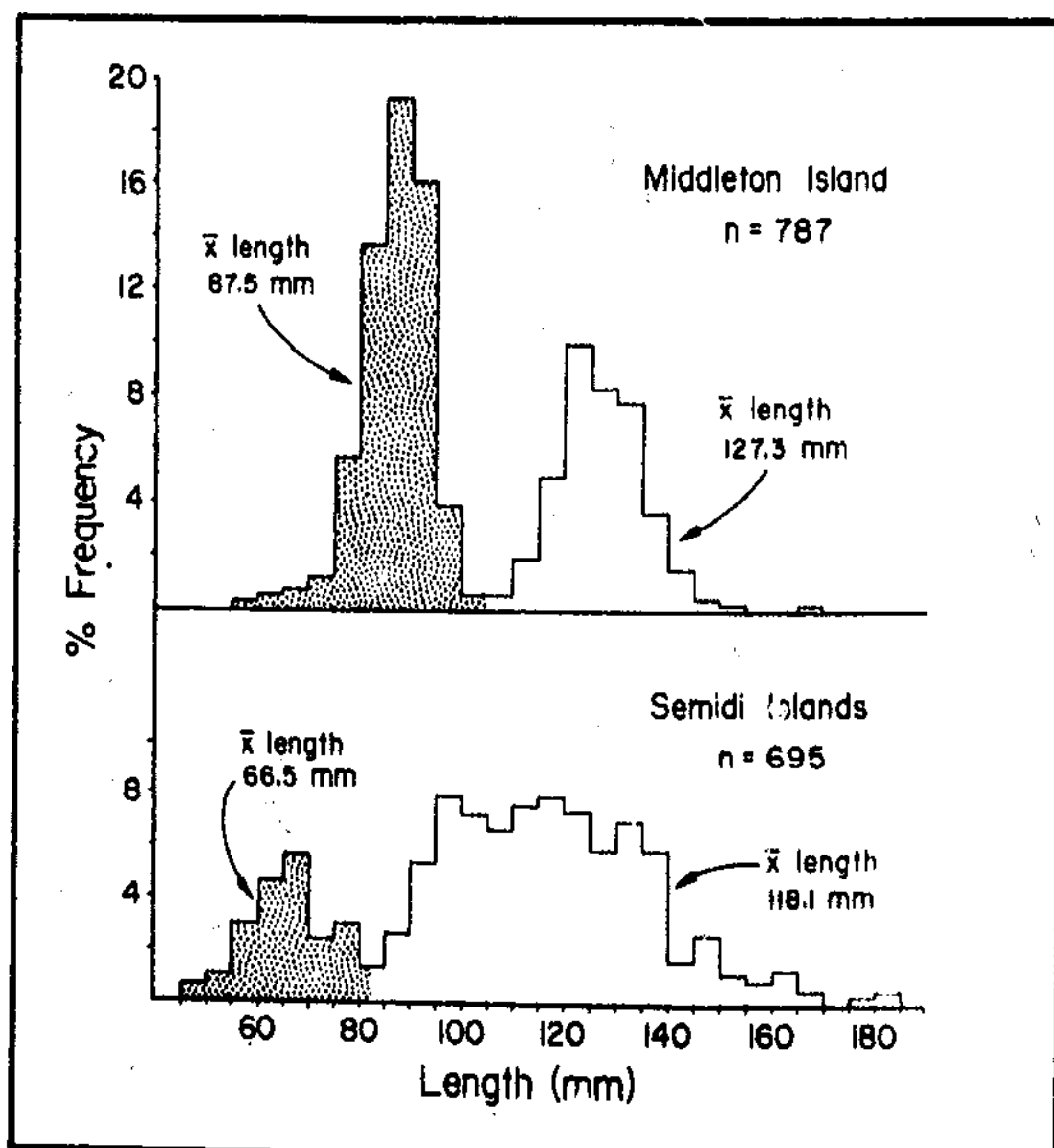


other variables (load-size, sampling date, and percent total sandlance) were controlled. Thus, a tendency for parents of older chicks to deliver larger fish selectively appears to be real.

6.4.3. Heterogeneity in species and age composition of burrow-loads — Since load-size was correlated with species composition and the proportional amounts of first-year and older sandlance, I examined variability in these characteristics in relation to samples collected on the same night, on successive nights, and in different sampling periods. Chi-square tests for heterogeneity of species composition within nights are limited to three nights at the Semidi Islands when substantial numbers of prey other than sandlance (mostly capelin) appeared in the samples. When capelin were available, they did not occur uniformly in all samples, but tended to show up disproportionately in a few (Table 6). Similarly, loads tended to consist of one age-class of sandlance or the other on nights when both classes were well represented (Table 7). One group or the other was largely absent on a few nights (dates excluded from the analysis).

Because both aspects of load composition varied significantly within nights, I used the nonparametric Kruskal-Wallis analysis of variance to test the significance of variation between nights and between sampling periods. Species composition (Table 6) was expressed as the percentage (by weight) of sandlance in each sample and age composition (Table 7) as the proportion of second-year or older sandlance. Again, there was significant heterogeneity in these characteristics between samples collected on successive nights and among samples collected during different stages of the season. The percentage of tests in which the

Figure 8
Comparison of length frequencies of Pacific sandlance in food samples from Middleton Island, 1978, and the Semidi Islands, 1979. Fish in the stippled area were assigned to the first-year age-class; fish in the unshaded area were considered second-year or older



null hypothesis is rejected is less than for samples collected on the same night, just as most variation in load-sizes occurred within nights (Table 3).

6.4.4. Influence of weather on feeding rates — One additional factor that may influence feeding rates is wind and associated sea conditions. Fortunately, each sampling period at the Semidi Islands included one windy and one calm night (Fig. 9b). On windy nights, wind velocity varied between about 20 and 50 km/h. For this analysis I treated wind as a nonmetric variable with two categories, windy or calm. I used an analysis of covariance to control for the increase in feeding rate as chicks aged. Results indicated that wind reduced mean load-size by about 11 g overall, a highly significant effect (Table 8).

My record of weather at Middleton Island is incomplete, but wind speeds varied little, probably averaging between 10 and 20 km/h each night. Nevertheless, there was as much variation in mean load-size between nights on Middleton as at the Semidis (Fig. 9, Table 3), so the influence of wind speed on feeding rates remains uncertain.

7. Discussion

7.1. Feeding rates: means and variability

Studies of Rhinoceros Auklets in Washington (Richardson 1961, Cody 1973, Leschner 1976, Wilson 1977) and British Columbia (Vermeer *et al.* 1979) found mean bill-load weights in the range 29–37 g, though Leschner observed a mean of 19 g in 1 of 2 years. The average burrow-loads observed in my study are close to what one would expect if chicks were fed by one adult each night. Whether this was so or whether two adults brought smaller than usual bill-loads is not known. Thirty-three of 68

burrow-loads (49%) collected on Middleton Island and 32 of 82 burrow-loads (40%) collected at the Semidis weighed more than 40 g and probably included two deliveries.

Table 4

Pearson correlation coefficients among load-size and several independent variables. All values above the diagonal are for Middleton Island; values below are for Semidis

		Weight of load	Age of chick	Sampling date	% total sandlance	% large sandlance*
Weight of load	<i>r</i>	—	0.066	0.055	0.332	0.411
	df	—	66	66	23	66
	<i>P</i>	—	0.295	0.329	0.048	0.001
Age of chick	<i>r</i>	0.344	—	0.320	0.096	0.339
	df	80	—	66	23	66
	<i>P</i>	0.001	—	0.004	0.321	0.002
Sampling date	<i>r</i>	0.235	0.729	—	0.135	0.300
	df	80	80	—	23	66
	<i>P</i>	0.017	0.001	—	0.260	0.006
% total sandlance	<i>r</i>	0.634	0.283	0.368	—	0.145
	df	11	11	11	—	21
	<i>P</i>	<0.001	0.033	0.008	—	0.254
% large sandlance*	<i>r</i>	0.361	-0.079	-0.188	0.648	—
	df	24	24	24	18	—
	<i>P</i>	0.035	0.351	0.178	0.001	—

*Weight of large sandlance as a percentage of total sandlance in the load

Table 5

Partial correlations of load-size with selected variables from Table 4

Area	Correlated variable	Variables controlled	<i>r</i>	df	<i>P</i>
Middleton	% total sandlance	Age of chick, sampling date	0.543	21	0.050
	% large sandlance	Age of chick, sampling date	0.417	61	<0.001
Semidis	Age of chick	Sampling date	0.260	79	0.010
	Sampling date	Age of chick	0.036	79	0.379
	% total sandlance	Age of chick, sampling date	0.604	39	0.001
	% large sandlance	Age of chick, sampling date	0.426	22	0.019

Table 3

Composition of the variance in weight of burrow-loads illustrated in Figure 9

Source of variation	Middleton Island		Semidi Islands	
	% of total variation	<i>P</i>	% of total variation	<i>P</i>
Between sampling periods	0.6	0.466	17.7	0.240
Between nights, within sampling periods	21.4	0.016	20.1	0.002
Within nights, between individuals	78.0		62.2	

Table 6

Heterogeneity of Rhinoceros Auklet food samples with respect to the proportion of sandlance per load

Area	Source of variation	Test	Date(s)	χ^2	df	<i>P</i>
Middleton	Between nights (within periods)	Kruskal-Wallis	26–27 July	4.7	1	0.031
			1–2 Aug	5.6	1	0.018
			8–9 Aug	1.4	1	0.233
			15–16 Aug	0.1	1	0.748
	Between sampling periods	Kruskal-Wallis	26 July – 16 Aug	9.7	3	0.021
Semidis	Between samples (within nights)	Chi ²	18 July	12.4	5	0.030
			19 July	67.9	14	0.001
			29 July	48.2	14	0.001
	Between nights (within periods)	Kruskal-Wallis	18–19 July	0.01	1	0.901
			28–29 July	3.5	1	0.063
			10–11 Aug	0.3	1	0.577
	Between sampling periods	Kruskal-Wallis	18 July – 11 Aug	23.4	2	0.001

The quantity of food delivered daily increased with the age of the nestling. Harris (1978) and Ashcroft (1979) showed that the rate of food consumption in Atlantic Puffins increased with age to a point, then declined during the last 2 weeks of the nestling period. No such pattern is evident in my data for Rhinoceros Auklets, but older nestlings may have been inadequately sampled. I assumed the relationship to be linear.

Additional variation in feeding rates presumably reflected changes in prey availability. Variation occurred both within and between nights, as did changes in the relative amount and size distribution of sandlance in the samples. My interpretation is that movements of this prey species, particularly the older individuals, largely determined the foraging success of Rhinoceros Auklets. When second-year and older sandlance became temporarily unavailable, the birds apparently were unable to compensate by switching to alternate prey.

7.2. Inferences about the population biology of sandlance

Recognizing that burrow-loads probably consisted of one or two bill-loads, I believe that strong heterogeneity in the composition of samples within nights simply resulted from small-scale patchiness in the distribution of prey. Birds probably encountered fish in fairly uniform shoals. Presumably, however, variation between nights and between sampling periods resulted from more pervasive temporal shifts in prey availability.

Carefully interpreted, the correlations shown in Tables 4 and 5 indicate age-specific patterns of movement and availability in sandlance. An increase in the proportion of large sandlance in the diet could come about in three ways. First, an increase in the absolute availability of large sandlance would increase load-size, total sandlance per load, and the relative proportion of large sandlance. Second, a decrease in the availability of small sandlance would increase the proportion of large fish, but total sandlance and load-size would decrease. Third, compensatory shifts could occur such that total biomass of sandlance remains the same but

Figure 9

Variation in the weight of burrow-loads of Rhinoceros Auklets: (a) Middleton Island, 1978; and (b) Semidi Islands, 1979, showing associated weather conditions

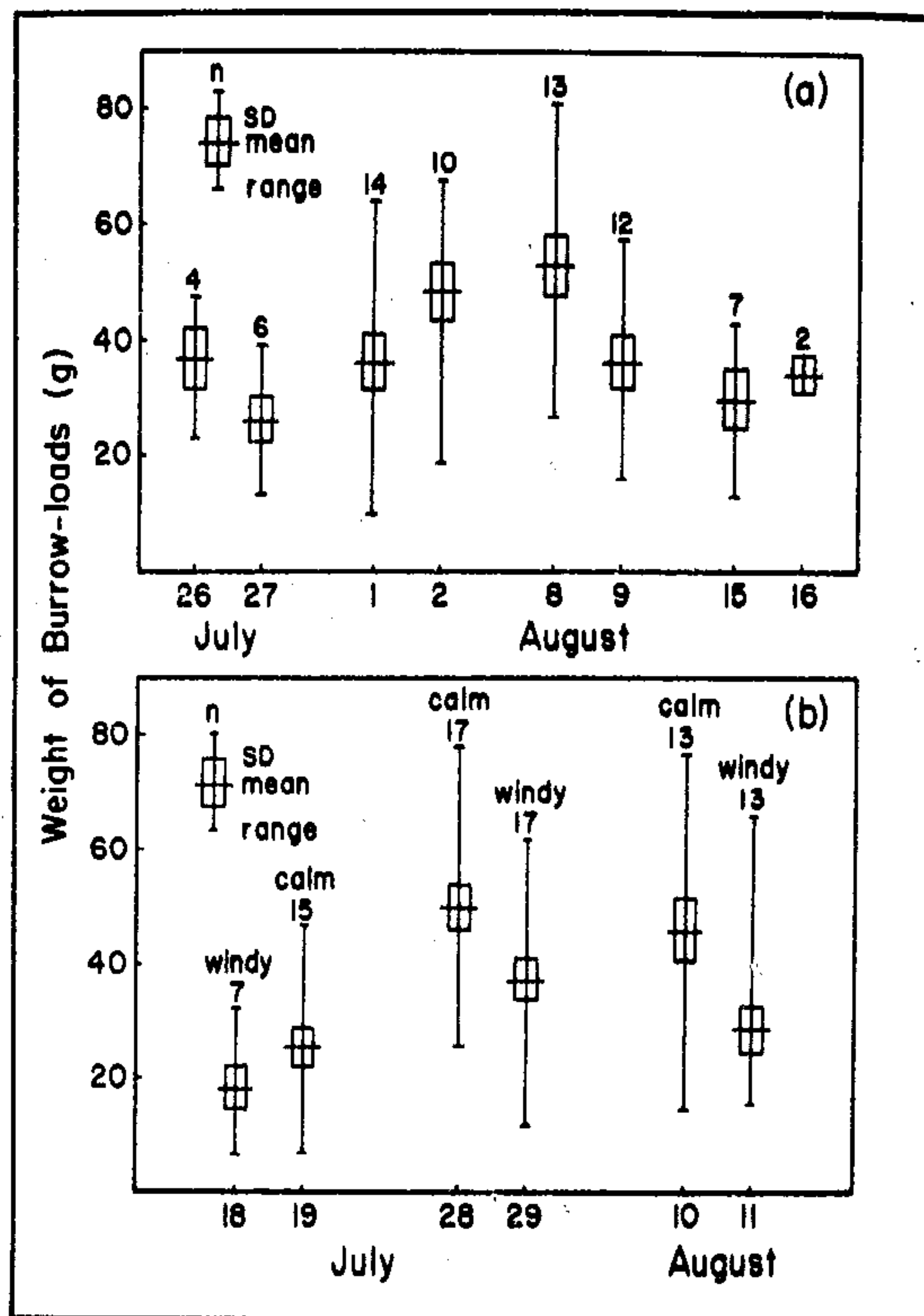


Table 7

Heterogeneity of Rhinoceros Auklet food samples with respect to the proportions of small and large size-classes of sandlance

Area	Source of variation	Test	Date(s)	χ^2	df	P
Middleton	Between samples (within nights)	χ^2	26 July	21.5	3	0.001
			1 Aug.	66.1	13	0.001
			2 Aug.	44.0	9	0.001
			8 Aug.	37.9	12	0.001
			9 Aug.	32.5	11	0.001
			15 Aug.	2.5	6	0.871
			16 Aug.	10.3	1	0.005
	Between nights (within periods)	Kruskal-Wallis	26-27 July	2.3	1	0.130
			1-2 Aug.	0.01	1	0.907
			8-9 Aug.	5.0	1	0.026
			15-16 Aug.	0.0	1	1.000
	Between sampling periods	Kruskal-Wallis	26 July - 16 Aug.	6.5	3	0.091
Semidis	Between samples (within nights)	χ^2	19 July	49.3	10	0.001
			29 July	85.7	14	0.001
			11 Aug.	82.0	12	0.001
	Between nights (within periods)	Kruskal-Wallis	18-19 July	2.1	1	0.149
			28-29 July	6.1	1	0.013
			10-11 Aug.	1.4	1	0.236
	Between sampling periods	Kruskal-Wallis	18 July - 11 Aug.	10.4	2	0.005

the relative abundance of large fish increases. In that situation, load-size and total sandlance would remain constant as the proportion of large fish increased. The results in Table 5 are consistent only with the first of these alternatives. The observed correlations apparently resulted from changes in the availability of second-year and older sandlance. Either the availability of first-year fish did not vary appreciably, or this variation exerted little influence on foraging success.

There was little difference between growth rates of first-year sandlance at Middleton Island and the Semidis. Furthermore, although sampling occurred 6 days earlier at the Semidis, that cannot account for the difference in size of first-year fish at the two study sites (Fig. 8). Therefore a difference in spawning time is the most likely explanation. The difference in the breeding phenology of puffins at the two sites paralleled this apparent difference in the phenology of their principal prey.

Judging from their greater abundance in food samples, second-year and older sandlance were more available at the Semidi Islands than at Middleton. I would expect this to affect the foraging success of Rhinoceros Auklets, yet feeding rates were similar at the two sites. The conclusions possible from a geographical comparison, however, are limited on this point. A longitudinal study at one site would be better because the ratio of age-classes in food samples provides no information about their absolute abundance, and we do not know the areas over which populations of sandlance are relatively discrete. The demography of sandlance is probably well represented, however, by sampling at one locality through time.

7.3. Differentiation of food habits among puffins

A salient result of this study is the degree to which Rhinoceros Auklets diverged from the other species in exploiting mainly older age classes of sandlance. Presumably this relates to the depth or distance from the colony at which the species feed, or to their differing daily activity schedules. (Rhinoceros Auklets deliver food to the young only at night, when the distribution of sandlance may be different than in daylight.) The populations of many pelagic fish are characterized by having relatively strong and weak year-classes resulting from large annual fluctuations in reproductive success (May 1974, Ricker 1975). Sandlance, at least in the North Sea, are no exception (Hart 1974). Whether the age-structure of prey populations differentially affects the breeding performance of puffin species would be interesting to explore. My data indicate that such an effect is likely, but the proper study of this phenomenon requires several years' observations on food habits and breeding success at mixed colonies. I expect the effect to be most evident where puffins exploit few species of prey, as appears to be true in the Gulf of Alaska.

Table 8

Composition of the variation in weight of burrow-loads explained by wind speed and age of the chick, Semidi Islands, 1979

Source of variation	% of total variation	P
Additive effects of chick-age and wind	21.5	0.001
(i) Wind, adjusted for chick-age	8.8	0.012
(ii) Chick-age, adjusted for wind	12.7	0.001
Interaction	2.8	0.093
Residual	75.7	

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10. Appendix

Evaluation of the collecting technique

There were no obvious indications that the use of muzzles on nestling Rhinoceros Auklets interfered with normal food provisioning by their parents, but further studies should include direct observations on marked burrows as a control. The technique caused the loss or injury of some chicks at Middleton, but this was eliminated with the use of cloth muzzles at the Semidis (Table 1).

In contrast, the method had a clear and immediate effect on the parental behaviour of Tufted Puffins, although the reasons for this difference are not clear. Mean load-size was depressed, and in most cases feeding ceased altogether. The parents must often have eaten the first bill-loads they brought after the chicks were muzzled, otherwise I would have found at least some food in most burrows. Feeding continued at undisturbed burrows on Middleton Island, and 10 control chicks grew normally throughout the season. Nearly total mortality occurred among Tufted Puffin chicks muzzled at the Semidi Islands, so the procedure was soon discontinued. Chicks that disappeared had apparently wandered out of their burrows. Although further trials with Horned Puffins are needed, it appeared that problems similar to those encountered in Tufted Puffins can be expected. If the technique caused subtle changes of parental behaviour in Rhinoceros Auklets, this would not necessarily alter any of the conclusions I have drawn, beyond the estimation of overall feeding rates.